

VENDIAN MICROFOSSILS IN METASEDIMENTARY CHERTS OF THE SCOTIA GROUP, PRINS KARLS FORLAND, SVALBARD

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ABSTRACT. Sedimentary rocks of the Scotia Group, Prins Karls Forland, Svalbard, have been metamorphosed to lower greenschist facies. Yet Scotia chert nodules contain abundant organic-walled microfossils belonging to at least seventeen taxa. Their black colour indicates that the fossils underwent substantial thermal alteration. However, it is suggested that preservation in a matrix of early diagenetic silica shielded them from the most destructive mechanical and chemical effects of metamorphism. Microbial mats and large acanthomorphic acritarchs suggest a coastal marine depositional environment; the acritarchs further indicate an early Vendian age for the sediments. The Scotia fossils bear a close resemblance to assemblages described from the Doushantuo Formation, China and elsewhere, demonstrating the broad geographical distribution of biostratigraphically important Vendian taxa. *Briareus* and *Echinospaeridium* are described as new genera; *Briareus borealis* is described as a new species, while *Echinospaeridium maximum* is proposed as a new combination.

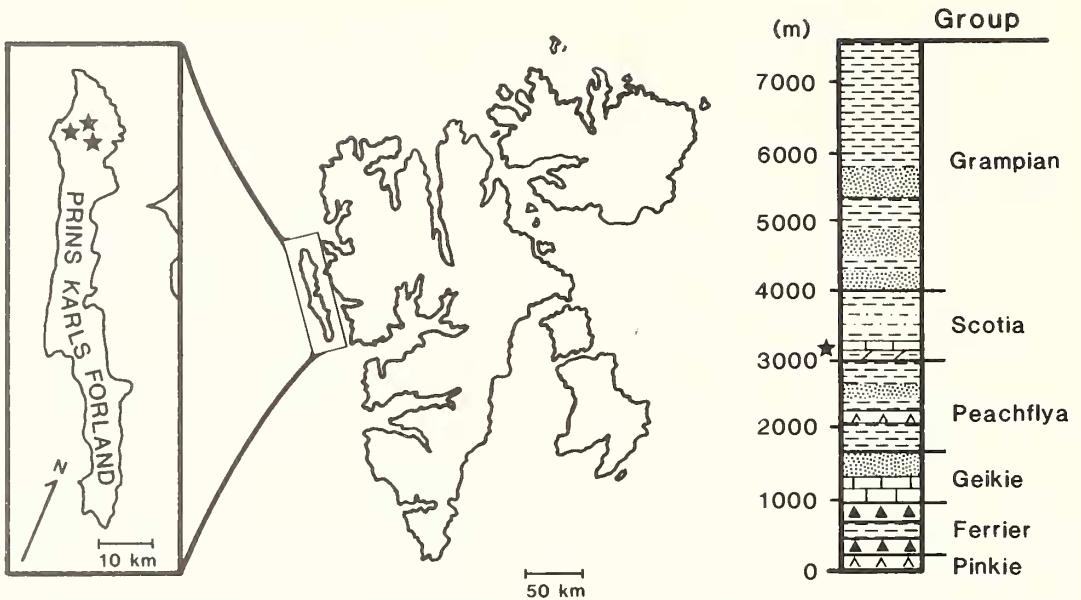
PRINS KARLS FORLAND, a narrow island situated off the west coast of Spitsbergen, is hardly a place where one might expect to find Precambrian fossils, since its Proterozoic strata were metamorphosed to lower greenschist facies or higher during Caledonian and Tertiary orogenesis. Yet identifiable microfossil populations are preserved, and they provide significant biostratigraphical, palaeoecological, and biogeographical data. Prins Karls Forland fossils were first reported by Knoll and Ohta (1988). In this paper, their systematic palaeontology is assessed and their geological and palaeobiological implications evaluated.

GEOLOGICAL SETTING

The pre-Carboniferous supracrustal succession of Prins Karls Forland (PKF) includes more than 7500 m of metamorphosed sedimentary rocks and volcanics (Harland *et al.* 1979). In the absence of fossils, there has been continuing uncertainty over the age of constituent lithological units. Even the most basic stratigraphical interpretation of superposition has been debated (compare Harland *et al.* 1979 with Hjelle *et al.* 1979).

Building on the work of Tyrrell (1924) and Atkinson (1956, 1960), Harland *et al.* (1979) divided the PKF succession into six lithological units. From base upward, they are the Pinkie metavolcanics, the tillite-containing Ferrier Group, the Geikie Group (sandstones and carbonates), the Peachflya Group (sandstones, phyllites, and metavolcanics), the Scotia Group (carbonaceous slates and carbonates), and the Grampian Group (turbidites, quartzites, slates, and conglomerate) (Text-fig. 1). Deposition clearly predated Caledonian deformation, and there is general agreement that the Ferrier tillites are glacio-marine sediments deposited during the Neoproterozoic Varanger (610–590 Ma) ice age (Harland *et al.* 1992). Further, the Grampian Group has been assigned an Ordovician or Silurian age on the basis of lithostratigraphical correlation with the fossiliferous Bullbreen Group on mainland Spitsbergen (Harland *et al.* 1992). However, the ages of the Geikie, Peachflya, and Scotia Groups have been unresolved, and even their stratigraphical position relative to the Varanger glaciation has been debated (summarized in Knoll and Ohta 1988). As described below, the PKF microfossil assemblage provides strong evidence that the lower Scotia Group (and, by implication, the Peachflya and Geikie Groups) was deposited during the early Vendian, prior to the major Ediacaran radiation of large animals.

The fossils occur in black chert nodules within the Baklia Formation, the lowermost unit of the Scotia



TEXT-FIG. 1. Sketch map of Svalbard, showing the location of Prins Karls Forland and, on the Forland, the locations of fossiliferous samples (indicated by stars). Also shown is a generalized stratigraphical column for the PKF succession, with the position of fossiliferous nodules in the Scotia Group indicated by a star.

Group. The Baklia succession includes black carbonaceous slates interbedded with carbonates (including oolites) and dolomitic siltstone (Harland *et al.* 1979); the nodules occur predominantly within the dolomitic siltstone units.

The oolitic carbonates could be either an *in situ* near-shore deposit or resedimented basal beds. Palaeontological features that support the first possibility include filamentous mats whose constituent microfossils are best known from Neoproterozoic rocks deposited in coastal marine settings (e.g. Knoll *et al.* 1991), shards of ripped-up and redeposited mats, and large, acanthomorphic acritarchs – forms that elsewhere predominate in lagoonal to shallow shelf environments (Butterfield and Chandler 1992).

The chert nodules are irregular to ellipsoidal and are often elongated subparallel to bedding. They consist of microquartz anhedral with variable amounts of euhedral dolomite, pyrite, and black organic material (Knoll and Ohta 1988). In some cases, blocky calcite replaced outer portions of the nodules during metamorphism. Early diagenetic silicification is indicated by the deformation of sedimentary laminae about the nodules, by the three-dimensional preservation of contained organic structures (Pls 1–6), and by the occasional accumulation of nodules in what appear to be lag conglomerates. Most nodules contain abundant organic matter arranged in irregular wavy, often discontinuous laminae. Some laminae are clearly mats; others include ripped up and re-deposited mat fragments and organic-rich muds.

Knoll and Ohta (1988) summarized petrological data suggesting that the fossiliferous beds were metamorphosed to lower greenschist facies. Chert appears to have protected microbial remains in at least two ways. The principal mechanical stresses of metamorphism were taken up by the less competent siltstones that surround the nodules. Also, the nearly impermeable chert shielded organic remains from recrystallization and the chemical ravages of metamorphic fluids. Consistent with its thermal history, organic matter in the nodules is black and often particulate. Because they are embedded in silica, the tiny bits of kerogen remain in place to define microfossil morphologies (e.g. Pl. 5, figs 3–4). However, the fossils cannot be isolated by maceration techniques.

THE MICROFOSSIL ASSEMBLAGE

Table 1 lists taxa identified in Scotia chert nodules. Densely interwoven mat populations of *Siphonophycus inornatum* (Pl. 2, figs 3, 5; Pl. 4, fig. 5) and *S. robustum* (Pl. 2, fig. 7) dominate the microbenthos, much as they

TABLE 1. Microfossil taxa in chert nodules of the Baklia Formation, Scotia Group, Prins Karls Forland, Svalbard.

<i>Microbenthos</i>	<i>Acritarchs</i> (probably planktonic)
<i>Obruchevella parva</i> Reitlinger	<i>Asterocapsoides sinensis</i> Yin and Li
<i>Obruchevella magna</i> Golovenok and Belova	<i>Briareus borealis</i> gen. et sp. nov.
<i>Siphonophycus inornatum</i> Zhang	<i>Echinosphaeridium maximum</i> comb. nov.
<i>Siphonophycus robustum</i> (Schopf) Knoll <i>et al.</i>	<i>Ericiasphaera spjeldnaesii</i> Vidal
<i>Siphonophycus</i> sp.	<i>Leiosphaeridia crassa</i> (Naumova) Jankauskas
<i>Polytrichoides lineatus</i> German	<i>Leiosphaeridia</i> sp.
<i>Wengania globosa</i> Zhang	<i>Papillomembrana compta</i> Spjeldnaes emend. Vidal
<i>Paratetraphycus giganteus</i> Zhang	? <i>Trachyhystrichosphaera</i> sp.
<i>Myxococcoides</i> spp. (may be planktonic)	

do in many Proterozoic assemblages. This does not necessarily indicate that two biological species covered the Proterozoic Earth; more likely it reflects the fact that sheath diameters in the 2–8 μm range are common among oscillatorian cyanobacteria (Schopf 1977). A third and much larger (cross-sectional diameter = 30–50 μm) *Siphonophycus* species occurs locally in mats (Pl. 2, fig. 4).

Helically coiled *Obruchevella* filaments occur as scattered individuals in both mat and non-mat settings. At least two distinct size classes are present: small (4–5 μm tube diameter) *O. parva* coils are rare (Pl. 1, figs 2, 5), but large (29–67 μm tube diameter) *O. magna* are second only to the smaller *Siphonophycus* species in abundance (Pl. 1, figs 1, 3, 5). Both large and small *Obruchevella* helices are widely distributed in Vendian and Lower Cambrian successions. They are generally interpreted as helical cyanobacteria, comparable to living *Spirulina* or *Phormidium* species (Luchinina 1975).

Other possible microbenthos are rare. A few mat horizons contain small coccoidal fossils, including *Myxococcoides* spp. (Pl. 2, figs 2, 7) and rare tetrads comparable to *Paratetraphycus giganteus* (Pl. 4, fig. 3) from the Vendian Doushantuo Formation of southern China (Zhang 1985). Scattered *Myxococcoides* individuals also occur in non-mat horizons and may be allochthonous.

Acritarchs, interpreted as the probable remains of planktonic protists, are rare but conspicuous in PKF cherts. Eight taxa have been identified. Given that each is represented by only one to three well preserved specimens, the recorded diversity is probably a strong function of sample size. Unusually large acanthomorphs dominate the acritarch biota. Six genera (each represented by a single species) have been recognized in addition to at least two leiosphaerid taxa (Table 1; Text-fig. 2). Once regarded as restricted to Phanerozoic rocks, acanthomorph-rich acritarch assemblages are now known from a growing number of Neoproterozoic localities (Knoll and Butterfield 1989). Like the microbenthic taxa, all of the PKF acritarch species also occur in the Doushantuo Formation, China (Yin and Li 1978; Awramik *et al.* 1985; Yin 1985, 1987, 1991; McMennamin 1990; Zhang Yun, pers. comm. 1990). Several also occur in the Pertatataka Formation, Australia (Zang 1988; Zang and Walter 1989), the Biskopåsen Conglomerate, Norway (Spjeldnaes 1963, 1967; Vidal 1990), and/or the lower Yudomian Kursovsky Formation, Siberia (Pyatiletov 1980; Pyatiletov and Rudavskaya 1985).

PALAEOGEOGRAPHICAL AND BIOSTRATIGRAPHICAL IMPLICATIONS

The most remarkable feature of the PKF assemblage is its taxonomic similarity to approximately contemporaneous assemblages deposited in south China and elsewhere. Palaeogeographical reconstructions of Neoproterozoic continental positions remain uncertain, but the occurrence of PKF-type fossils on at least five current plates makes it clear that the taxa in these assemblages had a wide distribution. This is unsurprising for cyanobacteria, as many extant species are cosmopolitan. Extant protists, on the other hand, have geographical distributions that range from local and endemic to intercontinental. Thus, broad geographical distributions for ancient eukaryotes cannot be assumed, but must be demonstrated empirically. In that the acanthomorphic acritarchs appear to be useful stratigraphically, the broad distribution inferred from recent discoveries is gratifying.

In China, the Doushantuo Formation occupies a distinctive stratigraphical position above the Varanger-age Nantuo Tillite and below beds containing Ediacaran metazoans (Yin 1985). The

palaeontologically comparable Pertatataka Formation, central Australia, occupies a similar stratigraphical position (Zang 1988), while the Biskopåsen Conglomerate, which shares two taxa in common with PKF and the Doushantuo Formation, was deposited during the early part of the Varanger epoch or slightly earlier (Vidal and Nystuen 1990).

The most problematic occurrence of PKF-type acritarchs is in the Kursovsky Formation of the Nepsk-Botuoba Anticline, interior Siberia. Conventionally, these beds are considered to be lower Yudomian (= lower Vendian) (Khomentovsky 1986). In their discussion of Kursovsky microfossils, Pyatiletov and Rudavskaya (1985) accepted this age assignment, but noted that several acanthomorphic acritarchs in the assemblage resembled typical Early Cambrian taxa except that the Kursovsky specimens tended to be much larger. More recently, Rudavskaya and Vasileva (1989) have reinterpreted the Kursovsky beds as Lower Cambrian. Based on personal observation, I believe that the large acanthomorphs found in this formation are not Cambrian species, but are indeed early Vendian taxa comparable to those from Prins Karls Forland, south China, and Australia. Specimens figured by Rudavskaya and Vasileva (1989) as *Baltisphaeridium varium* (pl. 2, fig. 8) closely resemble *Briareus borealis* described herein. Their *Baltisphaeridium primarium* (Rudavskaya and Vasileva 1989, pl. 2, fig. 3) is similar to a PKF specimen identified as *Asterocapsoides sinensis*, while the extremely large specimens assigned to *Baltisphaeridium strigosum* (pls 1–2) resemble *Comasphaeridium magnum* from the Doushantuo Formation (Zhang 1984) and some spinose acritarchs from the Pertatataka Formation (Zang 1988). In the samples I examined, I found no diagnostically Cambrian acritarchs. On the other hand, *Leiosphaeridia jacutia* with diameters exceeding 500 μm is common, as are other typically Proterozoic leiosphaerids. The entire assemblage is corroded in a puzzling way that is common in Vendian assemblages, but uncommon for younger acritarchs (see Germs *et al.* 1986). Thus, while additional research is required – and it may turn out that interior Siberian sections labelled 'Yudomian' may include both Vendian and Cambrian rocks – I believe it probable that the large acanthomorphic acritarchs of the Kursovsky Formation are early Vendian in age.

Thus, systematic comparisons suggest an early Vendian age for Scotia (and, by implication, Geikie and Peachflya) Group sedimentation. This conclusion is reinforced by the marked differences between PKF acritarchs and both older and younger assemblages. Acritarch assemblages of Late Riphean age are typically characterized by species of *Trachyhystrichosphaera* and *Cymatio-sphaeroides* (Knoll and Butterfield 1989; Knoll *et al.* 1991), as well as a number of distinctive sphaeromorphs, smaller acanthomorphs, and polygonomorphs (Vidal 1976; Vidal and Knoll 1983; Jankauskas 1989).

Most if not all of the large acanthomorph species that characterize immediately post-Varanger rocks disappear at or near the time of the main Ediacaran animal radiation. For example, despite intensive study, Vendian deposits of the East European Platform have not yielded large acanthomorphs of the PKF type, presumably because the main Vendian transgression across the platform began after the extinction of these acritarchs. Later Vendian acritarch assemblages are dominated by simple leiosphaerids, with only a minor representation of small spinose forms (Volkova 1968; Asseeva 1983; Germs *et al.* 1986; Jankauskas 1989). Acanthomorphic acritarchs diversified again during the Early Cambrian, but almost all Cambrian species are distinct from Neoproterozoic taxa (Volkova 1969; Vidal 1981; Downie 1982; Knoll and Swett 1987; Moczyłowska 1991).

In summary, the PKF acritarchs constrain interpretations of regional geology and also contribute to an emerging pattern of biostratigraphically significant evolutionary turnover among Neoproterozoic acritarchs.

SYSTEMATIC PALAEOLOGY

All specimens come from exposures of the Baklia Formation, Scotia Group, in northern Prins Karls Forland (Text-fig. 1). Baklia chert nodules are widely distributed on the island; specimens illustrated here come from 10° 45' E, 78° 41' N and 11° 26' E, 78° 57' N. All illustrations are from thin sections of Baklia chert deposited in the Paleobotanical Collections of the Harvard University Herbaria (HUHPC).

Kingdom EUBACTERIA Woese and Fox, 1977
Phylum CYANOBACTERIA Stanier *et al.*, 1978
Class HORMOGONEAE Thuret, 1875
Order OSCILLATORIALES Elenkin, 1949
?Family OSCILLATORIACEAE (S. F. Gray) Dumortier *ex* Kirchner, 1900
Genus OBRUCHEVELLA Reitlinger, 1948, emend. Yakshchin and Luchinina, 1981

Type species. Obruchevella delicata Reitlinger, 1948.

Discussion. *Obruchevella* was originally proposed for tightly and regularly coiled calcareous tubes of moderate size (filament diameter, 6–18 μm ; helix diameter, 30–50 μm) found in Lower Cambrian carbonates from Siberia (Reitlinger 1948, 1959). This circumscription was rather specific with respect to stratigraphical range, morphology, and preservational mode, but subsequent discoveries have broadened the observed range for all three parameters. Helical microfossils have a long (minimally Late Riphean to Devonian) stratigraphical range, although they are most common in uppermost Proterozoic and Lower Cambrian rocks. The fossils vary in size, density and regularity of coiling, numbers of coils per filament, and the presence or absence of a sheath. They may be preserved as organic sheaths compressed in shale or permineralized in silica, as pyritized compressions, phosphatic moulds or linings, or calcified helices. While carbonate deposition within and on sheaths may take place during the lifetime of the organism (under the biogeochemical influence of photosynthetic CO_2 removal and/or the activity of heterotrophic bacteria), no living cyanobacteria are known to be obligate carbonate precipitators (Pentecost and Riding 1986). Therefore, calcification is here considered to be a preservational mode rather than a systematically diagnostic character. Both biological and preservational patterns of variation are reflected in numerous generic names and specific epithets.

Although originally described as tubular foraminifera (Reitlinger 1948; Vologdin 1958), *Obruchevella* is now generally interpreted as cyanobacterial (Luchinina 1975). Systematic practice for extant helical cyanobacteria therefore provides a means of assessing the biological component of variation.

Living cyanobacteria that form regular helices occur in several genera, most notably *Romeria*, *Phormidium* (= *Lyngbya* Section *Spirocoleus* of Geitler 1930–1932), and *Spirulina* (Hindak 1985). *Romeria* is pseudofilamentous, consisting of mucilage-enveloped, spiraling rows of cells not connected by plasmodesmata. In contrast, *Phormidium* and *Spirulina* are both truly filamentous; they are differentiated on the basis of hormogonia and extracellular sheath formation – both present in *Phormidium* and strictly absent in *Spirulina* (Hindak 1985). Differences in size, cell shape, and habitat serve to differentiate species within these genera (Geitler 1930–1932), but coiling can vary widely within populations as a function of environmental variation and is therefore less useful as a systematic character (Hindak 1985).

Both Reitlinger (1948, 1959) and Vologdin (1958) described a number of genera that co-occur with *Obruchevella* and differ from it only in regularity of coiling or, in some cases, apparent differences in coiling that reflect varying planes of section. These include *Cavifera* (Reitlinger, 1948), *Lukashevella* (Vologdin, 1958), *Fluxurella* (Vologdin, 1958), and *Kordeella* (Vologdin, 1958), all of which are here considered to be synonyms of *Obruchevella*. *Tuvaellina* (Vologdin, 1958) and *Glomerovertella* (Reitlinger, 1948) may also belong in this group. Genera differentiated from *Obruchevella* on the basis of size, either small (*Avictuspirulina* Strother *et al.*, 1983) or large (*Spirellus* and at least some Cambrian forms attributed to *Glomerula* (Peel 1988)), are likewise considered synonymous with *Obruchevella*.

Most fossils assigned to *Obruchevella*, including the type, represent organically preserved or mineralized sheaths, and it is recommended that the generic concept be restricted to forms in which a sheath is definitely or probably present. Preservational mode is otherwise not considered an appropriate basis for splitting genera (e.g. Cloud *et al.* 1979; Shenfil 1980; Golovenok and Belova 1983; Golovenok *et al.* 1990; Jankauskas 1989; Sergeev and Ogurtsova 1989).

One helical microfossil whose distinct generic status appears justified is *Jiangispirellus* (Peel 1988). Peel considered *Jiangispirellus* to be trichomes *sans* sheath, and, therefore, different from *Obruchevella*. As noted above, this is consistent with neontological systematic practice.

An additional class of helically coiled microfossils is represented by *Heliconema* (Schopf 1968). As illustrated by Schopf (1968), the type species, *H. australiensis*, is not a coiled filament but a simple tubular sheath that unravelled along a spiral line of separation to form a helical *ribbon*. Such post-mortem alteration is well-known among oscillatorian cyanobacteria; it reflects the underlying architecture of the sheath (e.g. Geitler 1930–1932, p. 1066, fig. 679b; Golubic and Barghoorn 1977) but bears no necessary relationship to trichome coiling. Therefore, the genus is properly retained as a form taxon. The type specimen of a second species, *H. funiculum* (Schopf and Blacic 1971), is also a coiled ribbon, although in a restudy of original material, it was not possible to confirm this for two other illustrated specimens. The two *Heliconema* species described from the Soviet Union, *H. turukhanica* and *H. uralense*, are helical tubular sheaths; as is *H. bulbosa* from the upper Riphean Tindir Group, Alaska (Allison and Awramik 1989). These species should probably be transferred to *Obruchevella* (Jankauskas 1989).

Obruchevella parva Reitlinger, 1959

Plate 1, figs 2, 5

Description. Hollow cylindrical tube, non-septate, wound into a regular helix with no whorl expansion and a constant rate of whorl translation along the coiling axis; adjacent coils in contact with each other; cross-sectional diameter of tube = 4–5 μm , outer diameter of coil = 25–30 μm ; length of helix approximately 80 μm ; 15 or more turns per individual.

Material. Six measured specimens in thin sections of chert from the Baklia Formation.

Discussion. The PKF population falls near the lower size range of *O. parva*. Among described specimens it is most similar to a population described by Golovenok and Belova (1983) from the Vendian Chichkan Formation, Southern Kazakhstan. This species is a rare component of the PKF assemblage.

Obruchevella magna Golovenok and Belova, 1989 in Golovenok *et al.* 1989

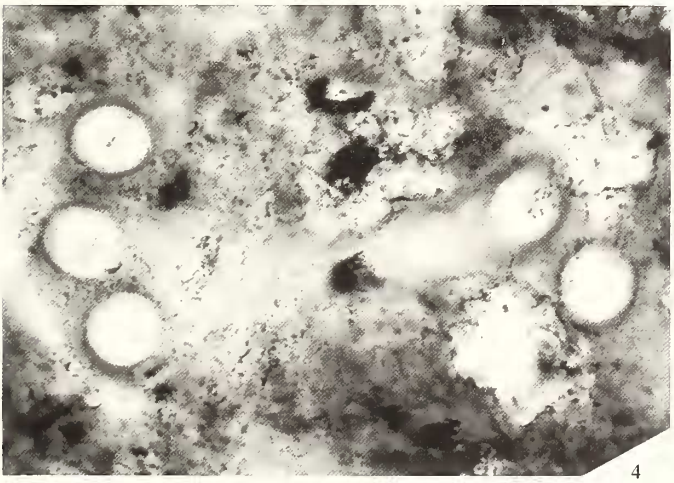
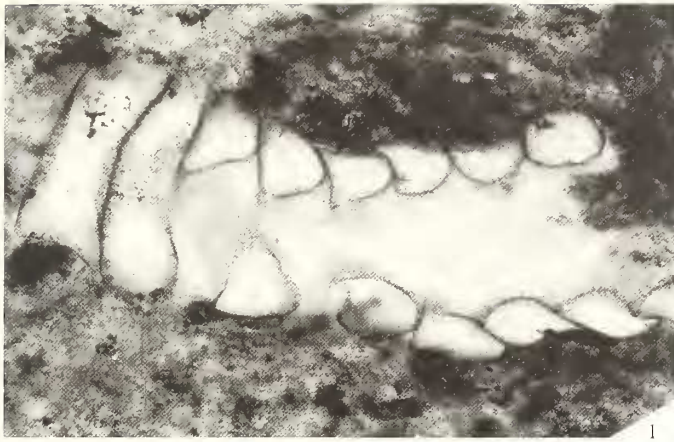
Plate 1, figs 1, 3, 5; Plate 4, fig. 6

Description. Hollow cylindrical tubes, non-septate, wound into a regular helix with no whorl expansion and a constant rate of whorl translation along the axis of coiling; adjacent coils in contact with each other or nearly so. Tubes 29–67 μm in cross-sectional diameter; outer diameter of coils 140–350 μm ; length of helix up to 450 μm . Commonly 3–4 coils, but up to 10. Wall commonly 1–2 μm thick, perhaps as a result of early diagenetic mineralization. Tubes may contain trichome fragments consisting of shrunken disc-shaped bodies arranged in a single row.

Material. Fifty measured specimens in thin-sections of chert from the Baklia Formation.

EXPLANATION OF PLATE I

- Fig. 1. *Obruchevella magna*. HUHPC 62426, Slide PKF-13, England Finder coordinates R48/0, $\times 200$.
 Fig. 2. *Obruchevella parva* and *Leiosphaeridia crassa*. HUHPC 62296 and 62427, Slide 72Gj76-2, England Finder coordinates 049/0, $\times 400$.
 Fig. 3. *Obruchevella magna*. HUHPC 62428, Slide PKF-5C, England Finder coordinates H51/4, $\times 200$.
 Fig. 4. *Obruchevella magna*. HUHPC 62298, Slide 72Gj76-3G, $\times 400$.
 Fig. 5. *Obruchevella parva*. Higher magnification photograph of specimen illustrated in Figure 3, $\times 800$.
 All specimens from the Baklia Formation, Scotia Group, Prins Karls Forland, Svalbard.



Knoll, *Obruchevella*, *Leiosphaeridia*

Discussion. *Obruchevella magna* is common in PKF chert nodules, generally occurring as isolated individuals. Comparably large *Obruchevella*-like fossils have been described from Vendian shales under the name *O. crassa*, *O.* (= *Volyniella*) *inviolata*, and *Volyniella rotundata* (Kolosov 1984); in Vendian and Lower Cambrian phosphorites as *Obruchevella* sp. (Wang *et al.* 1983), *O. magna*, *O. gigantea* (Golovenok *et al.* 1989), *Spirellus* (= *Glomerula*) *shankari* (Peel 1988), and *Spirellus columnaris* (Jiang in Luo *et al.* 1982); and in carbonates as *Obruchevella* sp. (Cloud *et al.* 1979). Considering the relatively small number of specimens reported, the number of published names is both impressive and frustrating. Depending on the logic employed, one might justify any of several species names for classification of the PKF forms.

O. magna Golovenok and Belova, in Golovenok *et al.* 1989 is accepted here, because among well-described and illustrated materials, this population is most similar to the Svalbard population. Restudy of *O. crassa* Kolosov (1984) may show this to be a senior synonym, but existing illustrations are not clear enough to apply the name with conviction. *O. magna* was originally reported from silicified Vendian phosphorites of the central Urals, where it occurs with somewhat larger specimens segregated as *O. gigantea* by Golovenok and Belova (in Golovenok *et al.* 1989). PKF fossils span the morphological range defined by end member *O. magna* and *O. gigantea*.

The PKF fossils also resemble phosphatic forms from Greenland described as *Spirellus shankari* by Peel (1988), and this designation might be preferred on grounds of seniority. However, as the type *Spirellus shankari* (originally described as *Glomerula shankari* from the Krol Formation, India, by Singh and Shukla 1981) reaches the much larger coil diameter of 1 mm, I am reluctant to apply that name to the PKF fossils. Whatever the name chosen, the Greenland specimens described by Peel (1988) are quite similar to the PKF helices.

The PKF specimens are also similar in form and dimensions to *Jiangispirellus groenlandicus* Peel (1988), but differ in that the latter consists of trichomes without identifiable sheaths.

Micro-organisms INCERTAE SEDIS
Genus MYXOCOCCOIDES Schopf, 1968

Type species. *Myxococcoides minor* Schopf, 1968.

Myxococcoides spp.

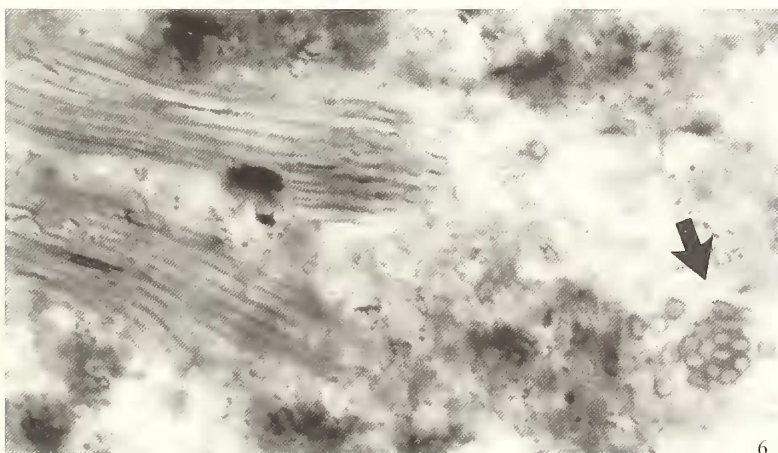
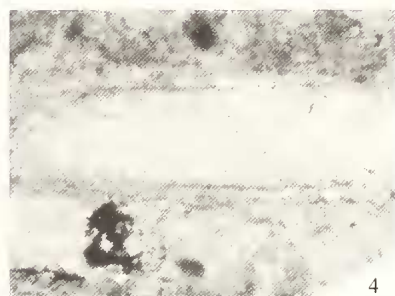
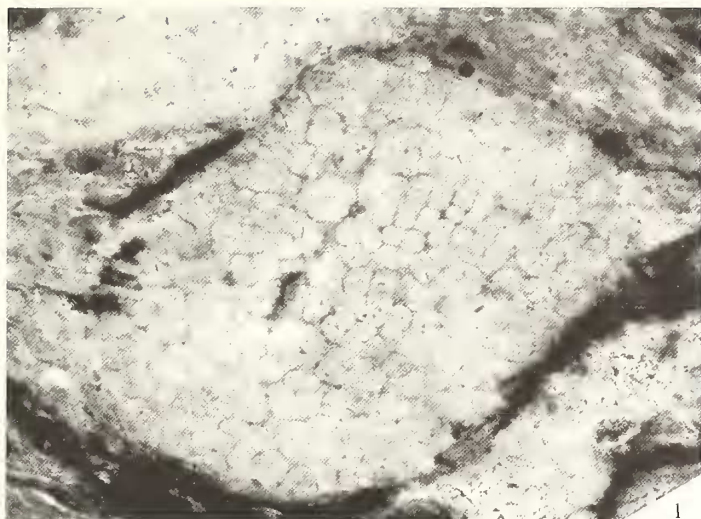
Plate 2, figs 2, 7

Discussion. Small spheroidal unicells occur sporadically throughout the PKF chert nodules. Their poor preservation discourages detailed taxonomic treatment, but all fit comfortably into the form genus *Myxococcoides*. These cells are difficult to interpret ecologically as well as systematically. Both *in situ* microbenthos and allochthonous (planktonic?) cells could be represented.

EXPLANATION OF PLATE 2

- Fig. 1. *Wengania globosa*. HUHPC 62429, Slide M-1, England Finder coordinates Y42/1, $\times 250$.
 Fig. 2. *Myxococcoides* sp. HUHPC 62430, Slide PKF-6C, England Finder coordinates W46/2, $\times 500$.
 Fig. 3. *Siphonophycus inornatum*. HUHPC 62296, Slide 72Gj76-2, England Finder coordinates T51/2; filaments in mat, oriented perpendicular to bedding, $\times 400$.
 Fig. 4. *Siphonophycus* sp. HUHPC 62431, Slide PKF-8, England Finder coordinates 049/1, $\times 400$.
 Fig. 5. *Siphonophycus inornatum*. HUHPC 62297, Slide 72Gj76-3F, England Finder coordinates N62/4 $\times 1000$.
 Fig. 6. *Polytrichoides lineatus*. HUHPC 62298, Slide 72Gj76-3G, England Finder coordinates L59/4, $\times 650$.
 Fig. 7. *Siphonophycus robustum* and *Myxococcoides* sp. HUHPC 62432 and 62296, Slide 72Gj76-2, England Finder coordinates S54/2, $\times 1000$.

All specimens from the Baklia Formation, Scotia Group, Prins Karls Forland, Svalbard.



Knoll, Vendian microfossils

Genus PARATETRAPHYCUS Zhang, 1985

Type species. Paratetranychus giganteus Zhang, 1985,

Paratetranychus giganteus Zhang, 1985

Plate 4, fig. 3

Discussion. *Paratetranychus giganteus* is a putative chroococcoid cyanobacterium described from the Doushantuo Formation (Zhang 1985). It is distinguished by the relatively large size of its constituent coccoids (10–21 μm) and by their characteristic arrangement in tight tetrads. Morphologically comparable tetrads are rare in the PKF assemblage.

Material. Two clusters of tetrads in thin sections of chert from the Baklia Formation.

Genus POLYTRICHOIDES German, 1974 emend. 1976 in Timofeev *et al.* 1976

Type species. Polytrichoides lineatus German, 1974 emend. 1976 in Timofeev *et al.* 1976.

Polytrichoides lineatus German, 1974 emend. 1976, in Timofeev *et al.* 1976

Plate 2, fig. 6

Discussion. *Polytrichoides* consists of non-septate tubes 2.5–6 μm in cross-sectional diameter; it differs from *Siphonophycus* in that five or more filaments are aggregated into tight, rope-like fascicles. *Polytrichoides* is rare within PKF mat associations.

Material. Three sheath fascicles in thin sections of chert from the Baklia Formation.

Genus SIPHONOPHYCUS Schopf, 1968 emend. Knoll *et al.*, 1991

Plate 2, figs 3–5; Plate 4, fig. 5

Discussion. *Siphonophycus* is a form genus for small, non-septate cylindrical tubes similar to the sheaths of oscillatorian cyanobacteria. As originally diagnosed, the genus applied only to tubes with cross-sectional diameters of 5 μm or more; however, Knoll *et al.* (1991) emended the genus and included within it species formerly assigned to *Eomycetopsis* and *Tenuofilum*. Type species in these genera differ from *Siphonophycus* species only in cross-sectional diameter. *Siphonophycus* differs from *Obruchevella* in the absence of a helical habit.

PKF cherts contain abundant ($N > 1000$) *Siphonophycus* filaments that fall into three size classes: *S. robustum* (2–4 μm in cross-sectional diameter), *S. inornatum* (5–8 μm), and *Siphonophycus* sp. (> 40 μm). All three populations occur as densely interwoven microbial mat assemblages, as well as isolated individual filaments. *Siphonophycus* is conventionally interpreted as a cyanobacterial fossil; while this is reasonable for the three populations preserved in PKF cherts, at least the smaller

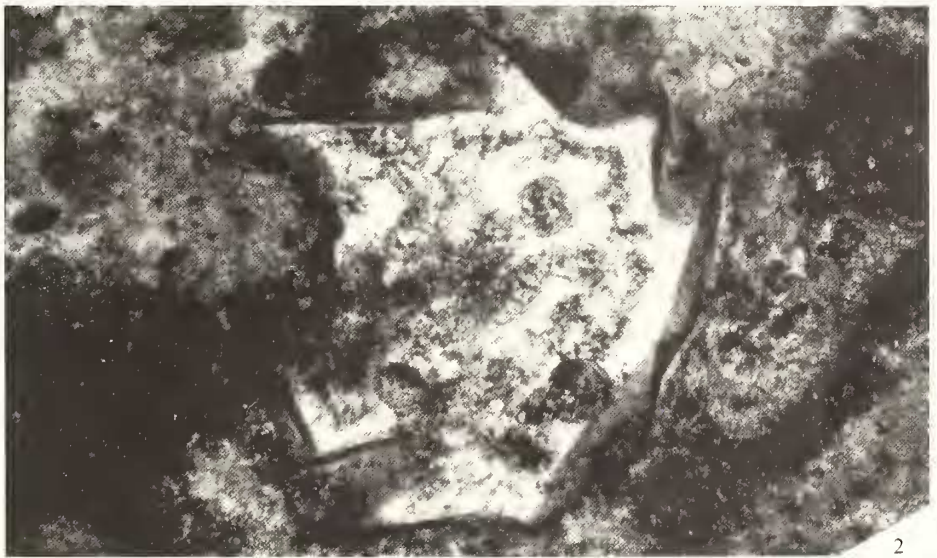
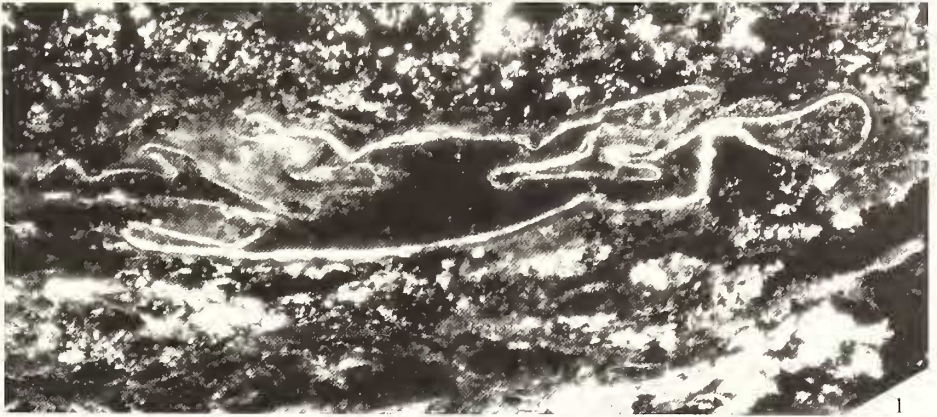
EXPLANATION OF PLATE 3

Fig. 1. *Leiosphaeridia* sp., HUHPC 62433, Slide M-3, England Finder coordinates R48/0; note that the thin wall is lined by a rim of clear silica, $\times 100$.

Fig. 2. *Leiosphaeridia* sp. HUHPC 62434, Slide PKF-5D, England Finder coordinates G54/4, $\times 100$.

Fig. 3. ?*Asterocapsoides sinensis*. HUHPC 62435, Slide PKF-5, England Finder coordinates S54/0; note broad conical processes at arrows, $\times 300$.

All specimens from the Baklia Formation, Scotia Group, Prins Karls Forland, Svalbard.



Knoll, *Leiosphaeridia*, ?*Asterocapsoides*

species cannot be differentiated unequivocally from the remains of green non-sulphur bacteria such as the mat-forming *Chloroflexus*. For this reason, the fossils are formally classified as *incertae sedis*.

Genus WENGANIA Zhang, 1989

Type species. Wengania globosa Zhang, 1989.

Wengania globosa Zhang, 1989

Plate 2, fig. 1

Description. Ellipsoidal structure 295 μm in maximum dimension, containing numerous cell-like units arranged in a pseudo-parenchymatous pattern; individual units 4–6 μm in diameter arranged into 10–15 μm packets of 4–8 cell-like units; 4–8 packets in larger assemblies, the whole giving an appearance of geometrically regular patterns of cell division.

Material. A single well preserved colony in a thin section of chert from the Baklia Formation.

Discussion. Zhang (1989) described a remarkable assemblage of multicellular structures preserved in phosphorite pebbles from the Doushantuo Formation. Several taxa were distinguished, including forms described as *Wengania globosa* and a related but unnamed form having geometrically regular cell division patterns like those of the PKF fossil. Re-examination of the Doushantuo specimens shows that these fossils experience a complex and varied history of cell degradation, compaction, and mineralization. I am reluctant to distinguish taxa or interpret patterns of apparent tissue differentiation in the absence of a thorough taphonomic analysis. Of the several (probably related if not synonymous) taxa described by Zhang (1989), *Wengania globosa* most closely matches the form displayed by the PKF fossil. Zhang's unnamed form A differs from the type *Wengania* principally in preservational mode. In *Wengania* cell contents are preserved, but walls or sheaths are not; in unnamed form A the reverse is true. The solitary PKF colony is assigned to *Wengania* not to differentiate it from other morphologies in the Doushantuo assemblage, but to note the relationship of this distinctive PKF fossil to a plexus of coeval Chinese forms.

Group ACITARCHA Evitt, 1963

Genus ASTEROCAPSOIDES Yin and Li, 1978

Type species. Asterocapsoides sinensis Yin and Li, 1978.

Asterocapsoides sinensis Yin and Li, 1978

Plate 6, figs 5–6

Description. Spheroidal vesicle 104 μm in diameter, bearing numerous broadly conical processes 18 μm high

EXPLANATION OF PLATE 4

Fig. 1. ?*Trachyhystrichosphaera* sp. HUHPC 62436, Slide PKF-7C, England Finder coordinates G49/2, $\times 150$.
 Fig. 2. *Myxococcoides* sp. and *Siphonophycus robustum*. HUHPC 62437 and 62438, Slide 72Gj76-3C, England Finder coordinates Q57/3, $\times 1000$.

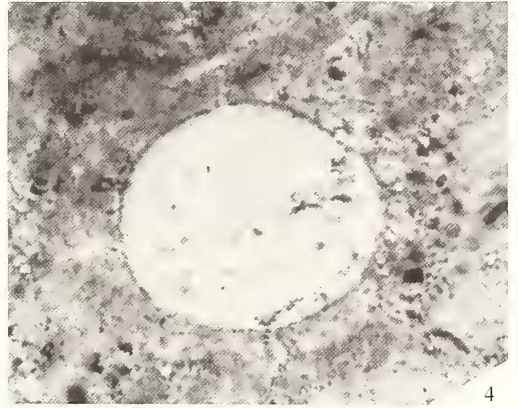
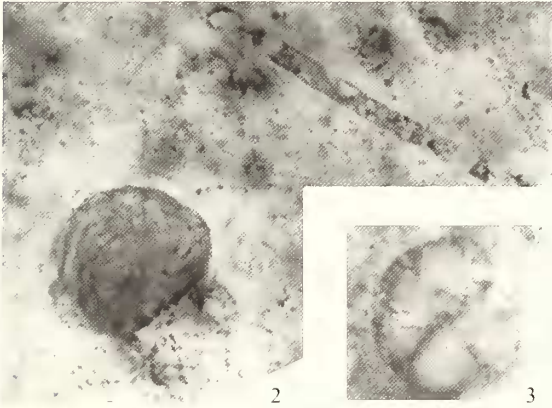
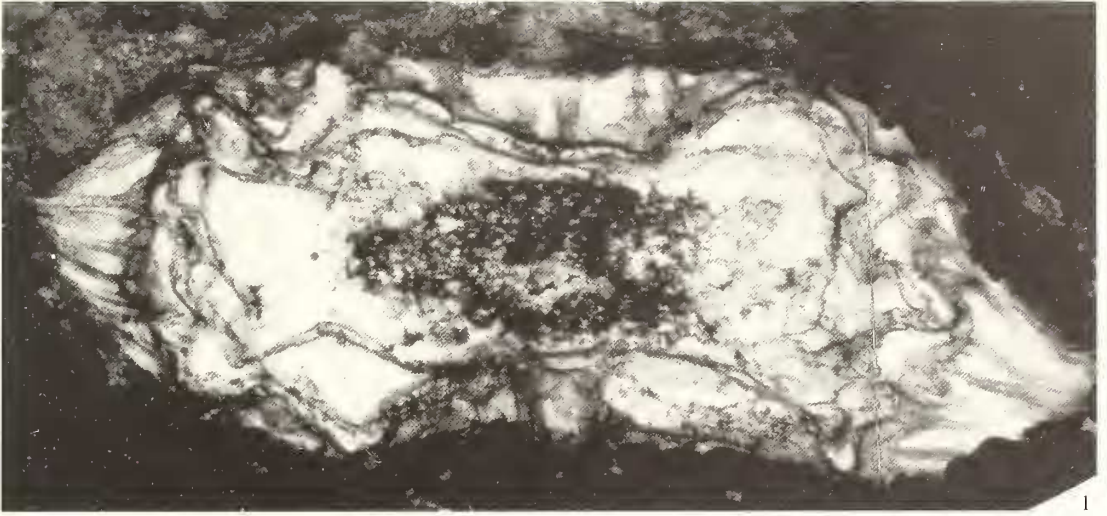
Fig. 3. *Paratetranychus giganteus*. HUHPC 62440, Slide PKF 12, England Finder coordinates V60/1, $\times 1000$.

Fig. 4. ?*Leiosphaeridia crassa*. HUHPC 62441, Slide PKF-7, England Finder coordinates P54/0, $\times 1000$.

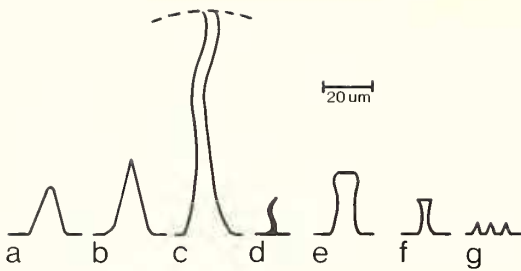
Fig. 5. *Siphonophycus inornatum* mat population. HUHPC 62442, Slide PKF 12, England Finder coordinates H59/0, $\times 150$.

Fig. 6. *Obruchevella magna*. HUHPC 62301, Slide 72Gj76-3C, England Finder coordinates R56/4; showing partly degraded trichome fragments within sheath, $\times 250$.

All specimens from the Baklia Formation, Scotia Group, Prins Karls Forland, Svalbard.



Knoll, Vendian microfossils



TEXT-FIG. 2. Diagram illustrating the differences in process morphology among PKF acanthomorphic acritarchs. All processes are hollow and communicate freely with the vesicle interior, except for D, which is solid. Process in C terminates at an outer membrane. A, *Asterocapsoides sinensis*. B, ?*A. sinensis*. C, ?*Trachyhystrichosphaera* sp. D, *Ericiasphaera spjeldnaesii*. E, *Papillomembrana compta*. F, *Briareus borealis*. G, *Echinospaeridium maximum*.

and 15 μm broad at the base (Text-fig. 2A); processes regularly arranged, with adjacent processes abutting at their bases; presence or absence of communication between process and vesicle interiors is unclear. A single PKF specimen is attributed to *A. sinensis*. The specimen is poorly preserved (Pl. 6, figs 5–6), but its overall morphology closely approximates that of the (somewhat larger; diameter = 325 μm) holotype from the Doushantuo Formation. A second, crushed specimen (Pl. 3, fig. 3; Text-fig. 2B) may also belong to this species. The specimen is 360 μm long and contains numerous hollow conical processes up to 65 μm long and 35 μm broad at the base.

Genus BRIAREUS gen. nov.

Type species. Briareus borealis sp. nov.

Diagnosis. Spheroidal vesicles > 100 μm in diameter, bearing numerous regularly arranged cylindrical processes; processes hollow, communicating freely with the vesicle interior, and flaring slightly at both base and apex; process length up to 20 per cent of vesicle diameter (Text-fig. 2F). Process-bearing vesicle may surround an inner, unornamented spheroidal vesicle. Excystment structures unknown.

Derivation of name. From the Greek 'Briareos', a hundred-armed giant, with reference to the large size and numerous processes of the fossils.

Discussion. *Briareus* is a distinctive morphotype within the PKF assemblage; it can be distinguished from co-occurring acanthomorphs by its distinctive process morphology (Text-fig. 2). Process form in *Briareus* is similar to that of the Early Cambrian genus *Skiagia* (Downie 1982; Moczydłowska 1991); however, processes in the younger genus do not communicate freely with the vesicle interior (Moczydłowska 1991). This alone would justify a generic distinction. Following precedent set by the segregation of the genus *Michrystridium* on the basis of size, it is here argued that the large size of *Briareus* also differentiates it from superficially similar Cambrian fossils. No described specimens of *Skiagia* have diameters that exceed 100 μm ; the PKF specimen and morphologically similar fossils from the Pertatataka Formation, Australia (Zang 1988) are all larger than 100 μm . Vesicle volume in *Briareus* exceeds that of *Skiagia* by more than two orders of magnitude. *Briareus* is known only from pre-Ediacaran rocks and is therefore separated stratigraphically from the oldest known *Skiagia* species by as much as 30–40 million years.

Briareus borealis sp. nov.

Plate 6, figs 3–4; Text-fig. 2F

Diagnosis Acanthomorphic acritarchs 100–200 μm in diameter; spheroidal vesicle bears numerous (45–60 visible around vesicle periphery) processes arranged regularly and separated by 5–10 μm ; processes hollow, communicating freely with vesicle interior, cylindrical, and expanded at base and apex; processes 11–13 μm long, *c.* 3 μm wide, and expanding to 4–5 μm at bases and apices.

Holotype. Specimen 62425 in the Paleobotanical Collections of the Harvard University Herbaria, illustrated in Plate 5, figures 3–4.

Derivation of name. From the Greek 'boreas', meaning 'northern', with reference to the high northern latitude of the type locality on Prins Karls Forland.

Type locality. Chert nodules of the lower Vendian Baklia Formation, Scotia Group, exposed in northern Prins Karls Forland, Svalbard (Text-fig. 1).

Material. A single well-preserved specimen in a thin section of chert from the Baklia Formation.

Discussion. *Briareus borealis* is a rare but distinctive component of the PKF assemblage. Morphologically comparable fossils occur in the Pertatataka Formation, Australia (Zang 1988; Zang and Walter 1989) and the Kursovsky Formation, Siberia (Rudavskaya and Vasileva 1989).

Genus ECHINOSPHAERIDIUM gen. nov.

Type species. *Echinosphaeridium maximum* (Yin, 1987) comb. nov.

Diagnosis. Spheroidal vesicle > 200 μm in diameter; vesicle surface echinate, densely covered by small (up to 5 μm long and 3 μm across at base) conical processes; processes unbranched, flexible, sharply pointed at distal terminus, and hollow, with process interiors connecting freely to the vesicle interior. Excystment structures unknown.

Derivation of name. From the Latin 'echinus', meaning spine-covered, and 'sphaera', meaning sphere, with reference to the shape and ornamentation of the fossil.

Discussion. Originally described from the Doushantuo Formation, these distinctive acritarchs were placed by Yin (1987) in the genus *Baltisphaeridium*. True *Baltisphaeridium* differs markedly from these Proterozoic fossils, necessitating reassignment to a different genus. Knoll *et al.* (1991) reported large echinate microfossils from the Upper Riphean Draken Formation, Spitsbergen, which they erroneously considered synonymous with *Baltisphaeridium maximum* and placed together with it in the new combination *Gorgonisphaeridium maximum*. The generic assignment reflects the observation that processes in the Draken specimens are solid; however, subsequent study of Doushantuo specimens clearly indicates that the Chinese fossils have hollow processes that connect freely with the vesicle interior. Therefore, they are not synonymous with the Draken fossils and the name *Gorgonisphaeridium maximum* is invalid. The genus *Echinosphaeridium* is proposed for acritarchs that combine the characters of extremely large size and densely arranged, hollow echinate processes.

Echinosphaeridium maximum comb. nov.

Plate 5, figs 5–6; Text-fig 2G

1985 *Baltisphaeridium* sp. Yin, p. 239, pl. 4, figs 4, 6.

1986 *Baltisphaeridium* sp. Yin, pl. 1, figs 11–12.

1987 *Baltisphaeridium maximum* Yin, pp. 439–440, pl. 14, figs 14–15.

Basionym. *Baltisphaeridium maximum* Yin, 1987, pp. 439–440, pl. 14, figs 14–15.

Holotype. The specimen figured by Yin (1987, pl. 14, figs 14–15).

Emended diagnosis. Spheroidal vesicles 200–650 μm in diameter; densely covered by short (3–5 μm long, 1.5–3 μm wide at base) echinate processes; mid-points of adjacent processes 4–5 μm apart; processes hollow, communicating freely with the vesicle interior. Excystment structures unknown.

Description. The single well-preserved PKF specimen is 638 μm in diameter and is clearly ornamented by

closely spaced (mid-points 5 μm apart) hollow echinate processes that communicate freely with the vesicle interior (Text-fig. 2G). Except for its somewhat greater diameter, this specimen is comparable to specimens from the type locality in China. Contrary to the view expressed by Vidal (1990), *E. maximum* cannot be considered synonymous with *Ericiasphaera spjeldnaesii* because the processes of the latter are solid.

Genus ERICIASPHAERA Vidal, 1990

Ericiasphaera spjeldnaesii Vidal, 1990

Plate 6, figs 1–4; Text-fig. 2D

Description. Spheroidal vesicles 125–130 μm in diameter that bear numerous regularly and closely spaced elongate processes. Processes are solid and flexible, with slightly conical bases and blunt or pointed apices; processes 11–13 (rarely 20) μm long, 2–3 μm across at base, and *c.* 1 μm in diameter above the base (Text-fig. 2D).

Material. Two well-preserved specimens in thin sections of chert from the Baklia Formation.

Discussion. Comparable acritarchs occur in the latest Riphean to early Vendian Biskopåsen Conglomerate, Norway (Vidal 1990); the early Vendian Pertatataka Formation, Australia (Zang 1988; Zang and Walter 1989); and the early Vendian Doushantuo Formation, China (Zhang Yun, pers. comm., 1990). The PKF fossils are smaller and have somewhat longer processes than the holotype, but they are otherwise comparable.

Genus LEIOSPHAERIDIA Eisenack, 1958 emend. Downie and Sarjeant, 1963

Type species. *Leiosphaeridia baltica* Eisenack, 1958

Discussion. Given its paucity of morphological characters, *Leiosphaeridia* (and similar, now mostly discarded, genera) has been an easy taxon to abuse. Many of the characters originally used to differentiate Proterozoic species and genera reflect the diagenetic alteration of vesicles (Vidal 1976; Damassa and Knoll 1986). In a recent comprehensive reassessment of Proterozoic leiosphaerids, Jankauskas and Mikhailova (in Jankauskas 1989) synonymized numerous taxa and divided those remaining according to vesicle size, wall thickness and surface texture. While doubtless not the last word on the subject, this does provide a stable framework of form species for the discussion of this ubiquitous, but morphologically simple, group of microfossils. At least two distinct populations are present in the PKF assemblage.

Leiosphaeridia crassa (Naumova) Jankauskas, 1989

Plate 1, fig. 4; Plate 4, figs 2, 4

Discussion. Leiospheres 30–70 μm in diameter with smooth walls *c.* 1 μm thick are moderately

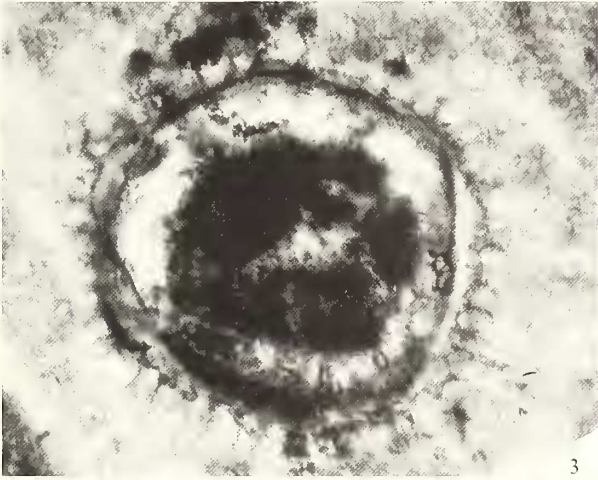
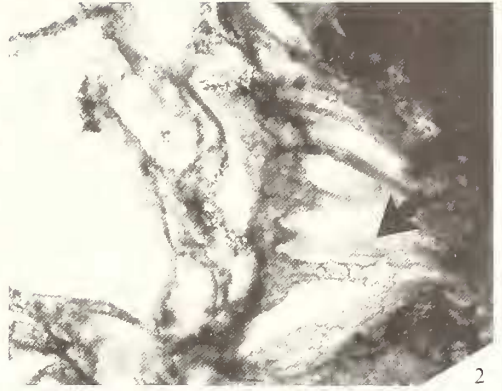
EXPLANATION OF PLATE 5

Figs 1–2. ?*Trachyhystrichosphaera* sp. Details of processes of specimen illustrated in Plate 4, figure 1; arrow in Figure 1 points to branching process; arrow in Figure 2 points to a well-preserved cylindrical process, $\times 250$.

Figs 3–4. *Briareus borealis* gen. et sp. nov. Holotype. HUHPC 62299, Slide 72Gj76-3A, England Finder coordinates J47/0. 3, $\times 333$. 4, detail of the specimen shown in Figure 3; arrow points to a well-preserved process, $\times 1000$.

Figs 5–6. *Echinospaeridium maximum* comb. nov. HUHPC 62445, Slide PKF-12, England Finder coordinates Q57/4. 5, $\times 140$. 6, $\times 500$.

All specimens from the Baklia Formation, Scotia Group, Prins Karls Forland, Svalbard.



Knoll, ?*Trachystrichosphaera*, *Briareus*, *Echinosphaeridium*

common in PKF cherts (20 specimens measured). In the Jankauskas/Mikhailova scheme, these fall into the morphological field of *L. crassa*. *Leiosphaeridia crassa* (= *Kildinella hyperboreica*) is among the most abundant of all Proterozoic acritarchs. By itself, this taxon carries little stratigraphical information.

Leiosphaeridia sp.

Plate 3, figs 1–2

Description. Spheromorphic vesicles 800–1300 μm in diameter; vesicle walls thin (c. 0.5 μm) and smooth, unless altered by diagenesis.

Material. Four measured specimens in thin sections of chert from the Baklia Formation.

Discussion. The Jankauskas/Mikhailova framework does not provide a name for very large, thin-walled leiosphaerids. In their graphical representation of leiosphaerid species classification, Jankauskas and Mikhailova (in Jankauskas 1989, pp. 24–25), indicated an upper limit of 1000 μm for *T. tenuissima*, but elsewhere (p. 81) they stated that the size range for this species is 70–200 μm . The Ordovician holotype is only 100 \times 106 μm (Eisenack 1958). Thus, it is debatable whether the PKF population and previously described *L. tenuissima* specimens belong to the same species. The poor preservation of the PKF specimens discourages their use as type of a new species, so for the purposes of discussion the population is here considered as *Leiosphaeridia* sp. The PKF assemblage contains no leiosphaerids with diameters of 100–800 μm , and no described population of Proterozoic *Leiosphaeridia* has both a mean diameter of 30–70 μm and a distributional tail that exceeds one millimetre. Thus, the recognition of two leiosphaerid taxa in the PKF assemblage is easily justified.

Genus PAPILLOMEMBRANA Spjeldnaes, 1963 emend. Vidal, 1990

Type species. *Papillomembrana compta* Spjeldnaes, 1963 emend. Vidal, 1990

Papillomembrana compta Spjeldnaes, 1963, emend. Vidal, 1990

Plate 6, figs 7–8; Text-fig. 2E

Description. The two PKF specimens encountered (one poorly preserved) are 224 μm and 240 μm diameter vesicles bearing numerous evenly spaced and tightly arranged processes. The processes are subcylindrical, hollow, open to the vesicle interior, and slightly expanded at both the proximal and distal ends; processes are 21–24 μm long, 11–12 μm across at the base and top, and 8–10 μm across at process-midpoints (Text-fig. 2E).

Discussion. In his original description, Spjeldnaes (1963) noted at least superficial similarities between *Papillomembrana* and dasycladacean algae, but cautioned that ‘much further work is

EXPLANATION OF PLATE 6

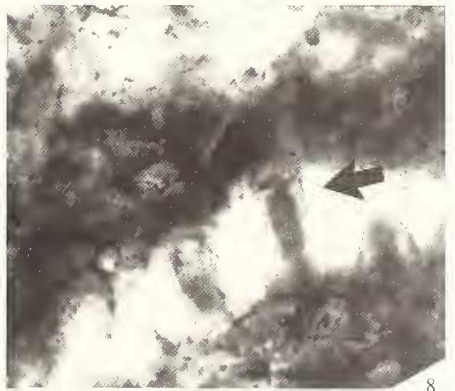
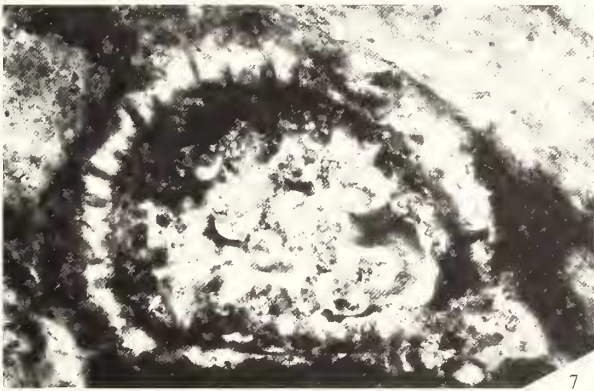
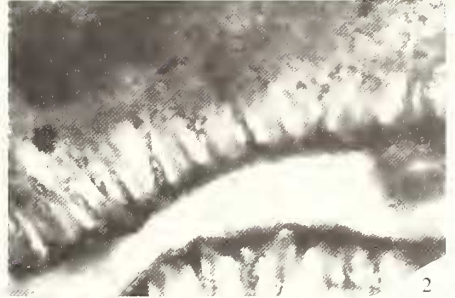
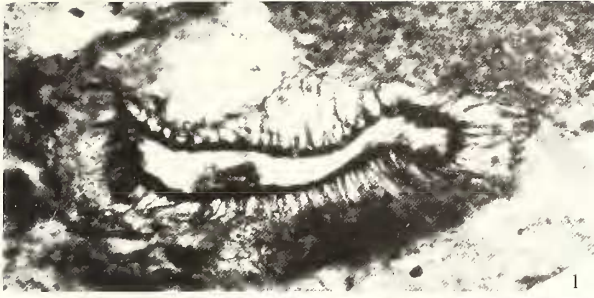
Figs 1–2. *Ericiasphaera spjeldnaesii*. HUHPC 62300, Slide M-4, England Finder coordinates H56/4. 1, \times 400. 2, \times 800.

Figs 3–4. *Ericiasphaera spjeldnaesii*. HUHPC 62446, Slide M-1, England Finder coordinates X47/1. 3, \times 333. 4, \times 666.

Figs 5–6. *Asterocapsoides sinensis*. HUHPC 62447, Slide PKF-8, England Finder coordinates, Q51/4. 5, \times 400. 6, \times 1000.

Figs 7–8. *Papillomembrana compta*. HUHPC 62448, Slide PKF-6, England finder coordinates W51/3. 7, \times 250. 8, \times 666.

All specimens from the Baklia Formation, Scotia Group, Prins Karls Forland, Svalbard.



Knoll, *Ericiasphaera*, *Asterocapsoides*, *Papillomembrana*

necessary to ascertain [its] systematic position'. Vidal's (1990) restudy of the type material demonstrated that *Papillomembrana* is a large acritarch. While this in no way clarifies its systematic affinities, it does establish that this remarkable fossil in one of a growing number of large acanthomorphs known to occur in Neoproterozoic strata (see also Knoll and Butterfield 1989). The PKF specimens are smaller than the holotype (vesicle diameter *c.* 518 μm), but are otherwise comparable. Given the large within-population size variation documented for other Neoproterozoic acanthomorphs (e.g. Knoll *et al.* 1991) and the somewhat smaller size of a second *Papillomembrana* specimen from the type locality (*c.* 331 μm), the relatively small vesicle diameters of the PKF fossils are ascribed to infraspecific variation.

This is the third reported occurrence of *Papillomembrana*. The type material comes from phosphoritic pebbles in submarine fan conglomerates of the latest Riphean to early Vendian Biskopåsen Conglomerate, southern Norway; additional specimens occur in the Vendian Doushantuo Formation, China (Yin 1991).

Genus ?TRACHYHYSTRICHOSPHAERA Timofeev and German, 1976 in Timofeev *et al.* 1976

Type species. *Trachyhystrichosphaera aimika* German, 1976 in Timofeev *et al.* 1976,

?*Trachyhystrichosphaera* sp.

Plate 4, fig. 1; Plate 5, figs 1–2; Text-fig. 2c

Description. Ellipsoidal vesicle 765 μm in maximum diameter bearing irregularly distributed processes that terminate distally at a thin outer membrane (maximum diameter = 980 μm); processes hollow and communicating freely with vesicle interior, up to 100 μm long and 33 μm broad at base, but decreasing distally within 20 μm to 4–8 μm in cross-sectional diameter (Text-fig. 2c); processes commonly truncated at outer membrane; processes predominantly solitary and unbranched, but can be branched (Pl. 4, fig. 1) or bunched in groups of two or three (Pl. 4, fig. 2). Thin ellipsoidal membrane internal to main vesicle wall.

Discussion. This distinctive taxon is represented by two specimens, one of them clearly preserved. The PKF specimens bear a clear morphological relationship to late Riphean acritarchs assigned to the genus *Trachyhystrichosphaera* (Timofeev *et al.* 1976; Knoll 1984; Knoll *et al.* 1991), but differ from described *Trachyhystrichosphaera* fossils by their substantially greater density of processes, greater regularity of process length, and somewhat expanded process bases. Given the small number and poor preservational state of the Scotia fossils, assignment to either a new species within *Trachyhystrichosphaera* or a new genus is not attempted. Comparable microfossils occur in the Doushantuo Formation (Yin and Li 1978; Awramik *et al.* 1985; McMennamin 1990).

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